# THE ANGLE OF DEVIATION FROM THE NORMAL VERTICAL POSITION AT WHICH STEMS SHOW THE STRONGEST GEOTROPIC RESPONSE.[1]

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## Introduction.

Sachs ('82) seems to have been the earliest botanist to pay particular attention to the relation between the angle of deviation in orthotropic plant organs and the strength of the geotropic response. He found, by experiment, that main roots of beans and oak seedlings inclined 8 or 10 degrees from the vertical, slowly or never came into the normal position, while if placed at an angle of 80 or 90 degrees, the growing parts curved 80 or 90 degrees in a few hours. In his "Lectures on the Physiology of Plants," Sachs ('87) also speaks of using in these experiments, thick, rigid, long internodes of such flower-stalks as attain considerable heights in short periods. The results led him to the conclusion that zones of similar developmental stages make various curvatures during the same time if they form various angles with the vertical. That is, the curvature is stronger, the more nearly the angle of deviation approaches to a right angle. If, therefore, this angle of deviation is a right angle, the maximum of growth-difference between the upper and lower sides is attained (Sachs, '74).

Miss Bateson and Francis Darwin ('88) used decapitated flower-stalks of *Plantago lanceolata* and *Brassica oleracea* and found, after numerous experiments, that in both Plantago and Brassica, the greatest curvature was made by the stems placed horizontally, less curvature by those inclined more than 90

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degrees, and least curvature in the stalks inclined less than 90 degrees.

Czapek ('95) took up the same line of experimentation as Bateson and Darwin, considering also the point which the other experimenters seem to have neglected, *i. e.*, the latent period of curvature in the various angles of deviation. His purpose was to determine at what angle of deviation it is possible to get the largest angle of geotropic after-effect, "the maximum reaction," for equally long induction periods. To eliminate specific differences, a variety of plants was used: Lupinus, *Faba vulgaris* (*Vicia faba*), Phaseolus, Pisum, and Zea seedling-roots, hypocotyls of Helianthus, and matured internodes of Secale. The general result of Czapek's experiments is given in the statement that the extent of the angle of after-effect curvature increases steadily from the normal vertical position, reaching a maximum at about 45 degrees above the horizontal or 135 degrees from the normal, in the case of roots; 45 degrees below the horizontal, or 135 degrees from the normal, in the case of stems; then falls from that point to the inversely vertical position, 180 degrees from the normal. The horizontal position is not, therefore, according to Czapek, the one in which the maximum reaction takes place.

In spite of his attempts in numerous experiments, even artificially lengthened for the purpose of enlarging small time-differences, Czapek could detect no noticeable difference, as to time of beginning curvature, in stems inclined from 20 degrees to 150 degrees, but in those inclined less than 20 degrees and in those whose angles of deviation were between the optimum for geotropic response and the inverted position, 180 degrees deviation, found a very considerable delay in the beginning of response.

Stone (: 00) experimented with dynamometers, measuring the after-effects of geotropic stimulation and found that in grass-nodes and in the roots of *Vicia faba*, all experiments gave similar results, indicating the horizontal position as that of greatest geotropic excitability. He further found the relationship between nodes at oblique angles and those horizontal to be proportional to the cosines of their angles.

Jost (:02), after making various experiments, agrees with Stone in doubting the validity of Czapek's results.

Just as this paper was ready to send to the publisher, there came to hand a preliminary report by Fitting (:04) in which the author states, among other results, that by a method somewhat similar to mine he has found the strongest geotropic effect when orthotropic plant members were placed in the horizontal position, that is, at 90 degrees from their position of equilibrium.

Because of this division of opinion, and since, in all cases, the experimenters had been led to favor one of the two angles of deviation, 90 degrees or 135 degrees, it seemed that other angles might be neglected and the issue drawn between these two. The present paper reports the results of a series of experiments made in the Botanical Laboratory of the University of Michigan under the direction of Professor Newcombe for the purpose of determining, in a considerable number of plants, at which of these two angles of deviation stems show the stronger geotropic response. Since the earlier work had dealt chiefly with seedling-roots and hypocotyls, the unbranched stems of actively growing young plants were selected as the material for use in most of these experiments.

## Method of Alternating Stimulation.

The two general methods used we shall call the "Alternating Stimulation" and the "After-effect" methods. It will be noticed that each differs somewhat from the methods of earlier workers. In all cases, except the first few experiments with Chrysanthemum which were made in the greenhouse where the plants were illuminated on all sides, the work was carried on in a dark-room whose temperature ranged from 20° to 24° C. (18.5° C. in one case).

It is evident that an orthotropic plant stem, if equally stimulated on opposite sides, will remain straight, but if unequally stimulated on the opposite sides, will become curved, and by the direction of its curvature indicate the stronger of the two stimuli. Since it was believed that the response of stems would be greater for stimulation in one of the two positions of

deviation in question than in the other, it was proposed to incline the plants first 90 degrees from the normal vertical position, then 135 degrees from the normal, but in the opposite direction, and to alternate between these two positions giving the same length of time and number of exposures in each, until a decided curve should result.

A special frame, devised by Professor Newcombe, made it possible to experiment with a considerable number of potted plants at one time. This frame was furnished with a hinged rack for holding the pots and this was so hung or supported that by turning it from one stop to another, through an arc of 225 degrees, the plants could be set first at an angle of 90 degrees, on one side of the vertical position, then at an angle of 135 degrees on the opposite side, or *vice versa*, and could be quickly and easily turned from one position to the other with a minimum of jarring.

The stems of the young plants selected were first tied to upright sticks or wires, leaving the upper, growing portions of the axes free to curve, while the weight of the older parts of the stems was supported to prevent all sagging when they were turned out of their normal position. In the case of several seedlings in one pot, all whose hypocotyls were not vertical were cut away at the outset. The pots were then firmly wedged in the frame, care being taken to keep the growing tips upright. When all was in readiness, the frame and its rack were turned so as to bring all the stems into one of the two positions desired, and alternation was begun.

## *Experimentation.*

Young plants of Chrysanthemum, Ageratum, Lavandula, Fuchsia, Heliotropium, and Coleus were used in these experiments; also seedlings of *Linum usitatissimum*, *Raphanus sativus*, *Brassica alba*, and *Helianthus annuus*. The process of alternation was continued from 2 to 7¾ hours according to the sensitiveness of the plants. When a noticeable curve appeared after an equal number of exposures in the two positions, the pots were set upright again and the direction of the stems was carefully noted.

The accompanying figure shows the frame turned on its side to bring the set of young Chrysanthemum plants into the upright position for observation at the close of one experiment. Plants 1, 3, and 4, numbering from the front, show typical curves. Other plants of the set gave equally good curves which do not show distinctly in this view.

During alternation experiments, the frame stands on the base

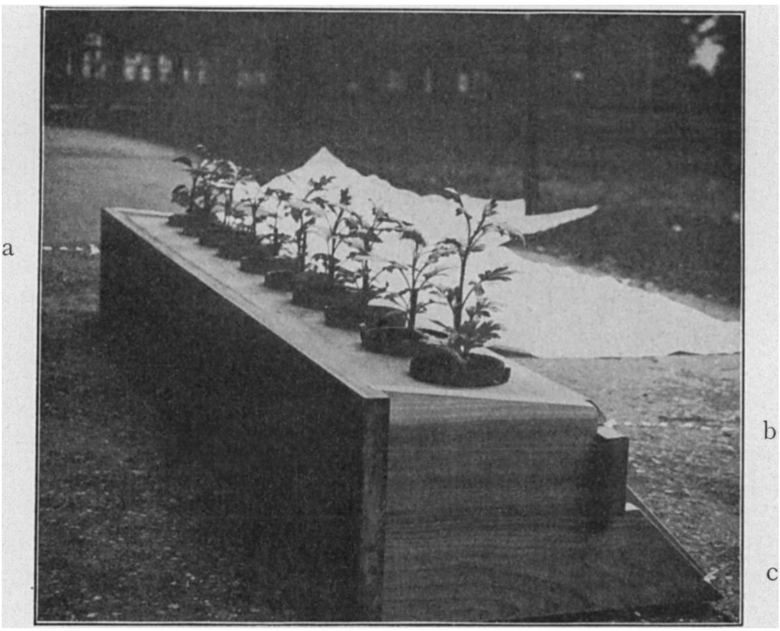


FIG. 1.— Plants in turning-frame. *a*, base; *b*, hinge-line; *c*, stop.

*a* and the shelf hinged at *b* hangs vertically while exposing the stems at 90 degrees from the normal position, then is turned over to stop *c* to make the exposure at 135 degrees from the vertical.

After experimenting in this way for some time, it was thought that an error might have entered through closing the experiments immediately after exposing the plants in the last position, thus allowing no time for the appearance of its resulting curvature, and, in effect, giving less exposure in one of the two positions than in the other. To remedy this, in the later

experiments the plants were allowed to stand upright for half an hour after the last exposure, before making the final observation. In no case did this modify results in favor of the deviation of 135 degrees, while with few exceptions, the plants, after this treatment, showed more pronounced curves in favor of the deviation of 90 degrees than they did at the close of stimulation. This was true whether alternation was begun from the position of 90 degrees deviation or from that of 135 degrees.

Marked differences in sensitiveness, indicated by the length of time required to produce curvature, were shown not only by plants of widely different genera but by different individuals of the same species and by the same individual at different times.

Of the 395 plants used in these experiments, 53 did not respond in the time given to the experiment, and are simply to be considered less sensitive than their fellows showing curvature. Of the 342 that did curve, 331 or 96.8 % responded better for the deviation of 90 degrees, 11 or 3.2 % only, for the deviation of 135 degrees.

*Table I. Results Obtained by Alternating Stimulation.*

| No. | Material. | Temp. | Time Hrs. Min. | No curvature. | Curvature at Deviation of 90 degrees | | Curvature at Deviation of 135 degrees |
|---|---|---|---|---|---|---|---|
| | *Young plants.* | | | | | | |
| 6 | Chrysanthemum | | 2 — 0 | 3 | 3 | | 0 |
| 6 | " | 13° C | 3 — 20 | 2 | 4 | | 0 |
| 5 | " | 18° C | 3 — 20 | 1 | 4 | 2 slight | 0 |
| 5 | " | 21° C | 3 — 40 | 0 | 5 | | 0 |
| 6 | " | 23° C | 3 — 0 | 0 | 6 | 1 slight | 0 |
| 10 | " | 22° C | 7 — 45 | 0 | 10 | | 0 |
| 9 | Ageratum | 20° C | 5 — 0 | 0 | 9 | | 0 |
| 5 | Heliotropium | 22° C | 4 — 0 | 0 | 5 | 2 very slight | 0 |
| 7 | Lavandula | 23° C | 3 — 40 | 0 | 7 | 1 slight | 0 |
| 7 | " | 22° C | 3 — 0 | 0 | 7 | | 0 |
| 3 | " | 22° C | 2 — 40 | 0 | 3 | 1 slight | 0 |
| 10 | Fuchsia | 25° C | 2 — 0 | 0 | 10 | | 0 |
| 10 | " | 18° C | 2 — 40 | 5[1] | 5 | | 0 |
| 9 | " | 20° C | 3 — 40 | 0 | 9 | | 0 |
| 9 | Coleus | 23° C | 3 — 0 | 0 | 7 | | 2 very slight |
| 2 | " | 22° C | 2 — 40 | 0 | 0 | | 2 very slight |
| | *Seedlings.* | | | | | | |
| 8 | Linum | | | 3 | 5 | | 0 |
| 150 | Raphanus sativus | 24° C | 2 — 0 | 3 | 145 | | 2 |

[1] After standing upright 30 minutes, all were curved in favor of 90 degrees deviation.

*Table I.— Continued.*

| No. | Material. | Temp. | Time Hrs. Min. | No curvature. | Curvature at Deviation of 90 degrees | 135 degrees |
|---|---|---|---|---|---|---|
| 29 [1] | Raphanus sativus | 22° C | 4 — 0 | 8 | 18 | 3 apparently |
| 22 [1] | " " | 21° C | 6 — 30 | 7 | 14 | 1 |
| 31 [1] | Brassica alba | 22° C | 4 — 0 | 3 | 28 | 0 |
| 25 [1] | " " | 21° C | 6 — 30 | 11 | 14 | 0 |
| 21 [1] | Helianthus annuus | 21° C | 6 — 30 | 7 | 13 | 1 |
| 395 | | | | 53 | 331 | 11 |

Number showing curvature, 342.
Percent of these showing curvature for deviation of 90 degrees, 96.8.
" " " " " " " " 135 " 3.2.

## After-effect Method.

By this method, orthotropic plant members are exposed to the one-sided action of gravitation by being placed out of their normal position ; but before a geotropic curve has time to appear, the plant is put upon the klinostat and so revolved that the further curving effect of gravitation is neutralized during the revolution. Thus any geotropic influence induced in the plant before the plant was placed on the klinostat has opportunity to manifest itself. If, now, the gravitation effect on plants differs according to the deviation of the plant from its normal position, we may expect the size of the after-effect angle attained on the klinostat to be greatest when the previous exposure of the plant was made at the angle of optimum stimulation. In other words, this method may possibly be used to aid in the discovery of the angle of optimum stimulation.

It was believed that results obtained by exposing stems for the short period to the gravity-stimulus would be more reliable than those of Czapek who forcibly prevented all curvature of the roots and hypocotyls used while exposing them for hours to the action of gravity in each of the two positions, and thus, it would seem, making it possible for the long continuance of a weak stimulus to equal the effect of a stimulus in reality stronger.

[1] Results quoted from Professor Newcombe by permission.

*Experimentation.*

The plants used in these experiments were prepared as in the preceding series, then fixed on klinostats with stems radial to the horizontal axes of rotation. One half of the number used were inclined 90 degrees, the other half, 135 degrees from the vertical, and both sets were held in position for a time somewhat shorter than the previously determined latent period for geotropic curvature in the species used. The subsequent influence of gravity was then removed by rotation on the klinostats for a time at least twice as long as the period of stimulation, and finally, the pots were set upright and the amounts of curvature made by the plants of the two groups were carefully compared. The number of individuals, as well as the number of species used in these experiments was smaller, and the results obtained were less satisfactory than in the experiments by the method of "alternating stimulation," but when any difference in after-effects could be observed, it was in agreement with the results of the alternation experiments. Ageratum, Lobelia, Chrysanthemum, and the seedlings of Linum showed greater curvature as the after-effect of stimulation at the angle of 90 degrees from the normal position than at 135 degrees.

*Table II. Results by After-effect Method.*

| Material. | Temperature. | Latent Period. | Time of Exposure. | Time of Rotation. | Greater Curvature for Deviation of |
|---|---|---|---|---|---|
| *Young plants.* | | | | | |
| Lobelia | 25.5° C | 30 min. | 20 min. | 40 min. | 90 degrees |
| Ageratum | 22.0° C | 20 " | 15 " | 40 " | 90 " |
| Chrysanthemum | 22.0° C | 30 " + | 30 " | 60 " | 90 " |
| *Seedlings.* | | | | | |
| Linum | 26.5° C | 25 " + | 25 " | 50 " | 90 " |

## Conclusions.

In conclusion it may be said that both the method of "alternating stimulation" and the "after-effect" method as I have used them in numerous experiments involving a greater number of species than other experimenters have reported, furnish remarkably strong evidence that stems respond better to the gravity stimulus when their angle of deviation from the normal position is one of 90 degrees than when it is one of 135 degrees; and since the question seems to have been narrowed to these two angles by earlier workers, it may further be claimed that the angle of deviation from the normal vertical position at which stems show the strongest geotropic response is one of 90 degrees.

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## Bibliography.

Bateson, A. and Darwin, F.

**'88.** A Method of Studying Geotropism. Annals of Bot., II, 65.

Czapek, F.

**'95.** Untersuchungen über Geotropismus. Jahrb. Wiss. Bot., XXVII, 283.

Fitting, H.

**:04.** Geotropische Untersuchungen. (Vorl. Mittheil.) Ber. Deutsch. Bot. Gesellsch., XXII, 361.

Jost, H.

**:02.** Die Perception der Schwerereizes in der Pflanze. Biol. Centralbl., XXII, 167.

Sachs, J.

**'74.** Ueber das Wachsthum der Haupt- und Nebenwurzeln. Arbeit. Bot. Inst. Würz., I, 454.

**'82.** Ueber orthotrope und plagiotrope Pflanzentheile. Arbeit. Bot. Inst. Würz., II, 240.

**'87.** Lectures on the Physiology of Plants. English translation.

Stone, G. E.

**:00.** Geotropic Experiments. Bot. Gazette, XXIX, 136.